

*The Dia-Heliotropic Attitude of Leaves as determined by  
Transmitted Nervous Excitation.*

By Sir JAGADIS CHUNDER BOSE, F.R.S., Director, Bose Institute, Calcutta.  
Assisted by SATYENDRA CHANDRA GUHA, M.Sc., Research Student,  
Bose Institute, Calcutta.

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The leaves of plants adjust themselves in various ways in relation to the incident light. The heliotropic fixed position is assumed by means of curvatures and torsions of the motor organ which may be the pulvinus, or the petiole acting as a diffuse pulvinoid. In some cases the motor organ alone is both perceptive and responsive; in others, the leaf blade does exert a directive action, the perceptive lamina and the motor organ being separated by an intervening distance. This directive action of the lamina has been found by Vochting in *Malva verticillata*, and by Haberlandt in *Begonia discolor*, and in several other plants. In connection with this it should be borne in mind that this characteristic does not preclude the possibility of the motor organ being directly affected by the stimulus. In a nerve-and-muscle preparation, the muscle is excited, not merely by indirect but also by direct stimulus. As regards the heliotropic adjustment of leaves, the stimulus of light acts, in the cases just mentioned, both directly and indirectly, the indirect stimulation being due to some transmitted effect from the perceptive lamina. We may regard the coarse adjustment to be brought about by direct, and the finer adjustment by indirect stimulation.

Certain leaves thus assume a heliotropic fixed position so that the blades are placed at right angles to the direction of light, the directive action being due to certain transmitted reaction, yet unknown. No explanation has, however, been forthcoming as regards the physiological reaction to which this movement must be due. Suggestions have been made that the dia-heliotropic position of leaves is of obvious advantage, since this position assures for the plant the maximum illumination. But such teleological considerations offer no explanation of the definite physiological reaction. It is, moreover, not true, as I shall show in the course of this paper, that there is anything inherent in the plant-irritability by which the surface of the leaf is constrained to place itself perpendicular to the incident light.

I have for many years been engaged in pursuing investigation on the subject, and have recently succeeded in discovering the fundamental reaction to which the directive movement is due. I shall be able to show that the

particular attitude assumed by the leaves is brought about by transmitted "nervous impulse," which impinges on the motor organ, which is not simple but highly complex; that there are several distinct impulses which react on the corresponding effectors grouped in the motor organ.

For a full and satisfactory explanation of the phenomena, it will be necessary to deal briefly with the characteristics of the motor organ and the nervous impulse which actuates it. It will also be necessary to show that the physiological reactions of the "sensitive" and "ordinary" plants are essentially similar. As a type of the former I shall take *Mimosa pudica*, and for the latter, *Helianthus annuus*. I propose to deal with the subject in the following order:—

I.—General description of the dia-heliotropic phenomena.

II.—Characteristics of the motor organ :

1. Mechanical response due to differential excitability of the pulvinus of *Mimosa* and pulvinoid of *Helianthus*.
2. Response to stimulation of adaxial and abaxial halves of the motile organ.
3. The mechanism of heliotropic curvature.
4. The diurnal movement.
5. Torsional response to lateral stimulation.

III.—The nervous mechanism in plants :

6. Receptor, conductor, and effector.
7. Localisation of nervous tissue in plants.

IV.—The transmitted nervous impulse :

8. Definite innervation.
9. The directive action of propagated impulse in heliotropic leaf adjustment.

#### I.—GENERAL DESCRIPTION OF THE DIA-HELIOTROPIC PHENOMENA.

Before entering into the experimental investigation of the subject, it is desirable to describe the dia-heliotropic phenomena, as typically exemplified by *Mimosa* and *Helianthus*. A photograph of the former is reproduced in fig. 1, *a*, in which the plant placed in a box had been exposed to the northern sky and not to direct sunlight. It will be seen that the leaves which directly front the light have been raised, and so placed that the sub-petioles, with their leaflets, are at right angles to the strongest illumination. The side or lateral leaves have, on the other hand, undergone appropriate torsions—the plane of the leaflets being adjusted perpendicular to the light. It will be noticed that in executing this, the petioles to the right and the left have undergone opposite torsions.

After the assumption of this position, the pot containing the plant was turned round through  $180^{\circ}$ . This brought about a new adjustment in the course of twenty minutes, the plane of all the leaflets being once more at right angles to the light. The new adjustment necessitated a complete reversal of the former movements and torsions. Such perfect adjustment is brought about by bright light from the sky, and not so well by direct sunlight, for reasons which will be given later.

In fig. 1, *b*, is seen the heliotropic adjustment of the leaves of sunflower, grown near a wall, the plant being exposed to light from the western sky. The adjustment is essentially similar to that seen in *Mimosa*. The lateral leaves,

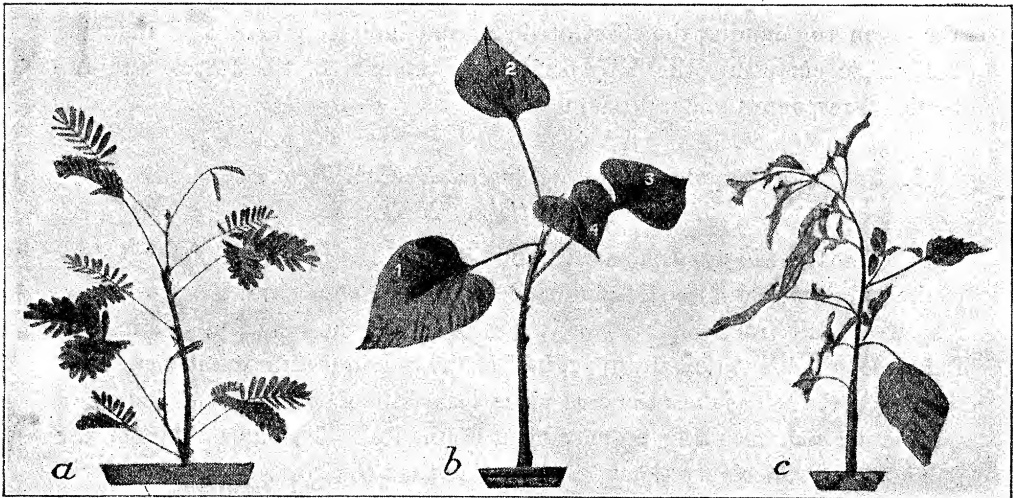


FIG. 1.—Dia-heliotropic adjustment of leaves : (a), in *Mimosa* ; (b), in *Helianthus annuus* ; and (c), in a different species of *Helianthus*. (From photographs.)

1 and 3, have undergone appropriate torsions—right-handed or left-handed—so that the leaf-blades placed themselves at right angles to the light. The leaf numbered 2 has been raised, placing its lamina perpendicular to the light. A contributing factor in this is the bending over of the stem, due to positive heliotropic curvature, which accentuated the rise of the leaf number 2. The same bending often causes an apparent fall of the leaf marked 4. When the stem is tied to a stake, the bending over of the stem is prevented; the leaf numbered 2 is then found raised by heliotropic action; but there is little or no fall of the opposite leaf.

I reproduce (fig. 1, *c*) another photograph of the heliotropic curvature and adjustment of a different species of sunflower, which was grown in the open. In the morning the plant bent over to the east and all the leaves exhibited

appropriate movements and torsions. In the afternoon the plant bent over to the west, all the previous adjustments and torsions being completely reversed. The plant continued to exhibit these alternate swings day after day till the movement ceased with age.

## II.—CHARACTERISTICS OF THE MOTOR ORGAN.

I have shown elsewhere (2) that there is no essential difference between the response of "sensitive" and "ordinary" plants. I shall now show that all the characteristics of the response of the leaf of *Mimosa* are also found in the leaf of *Helianthus*. These will be specially demonstrated as regards normal response and recovery, the response of adaxial and abaxial halves of the organ to stimulus, the effect of direct and indirect stimulus in inducing heliotropic curvature, the daily periodic movements of the leaves, and the torsional response to lateral stimulation.

### 1. *Mechanical Response due to Differential Excitability of the Pulvinus of Mimosa and Petiole of Helianthus.*

In *Mimosa*, owing to differential excitability of the upper and lower halves of the pulvinus, a diffuse stimulus, such as that of an electric shock, causes a responsive fall from which there is a recovery on the cessation of stimulus. It has been thought that the upper half of the pulvinus is inexcitable. I have shown (3) that this is not the case, since local stimulation by light induces a contraction and resulting up-movement of the leaf. The upper part of the pulvinus is about eighty times less excitable than the lower half.

*Experiment 1.*—In *Helianthus*, the entire petiole acts as a motor organ, of which the upper half is relatively less excitable. Diffuse stimulation by electric shock induces a responsive fall, followed by a recovery on the cessation of stimulus. The response-records thus obtained are very similar to those obtained with the leaf of *Mimosa*. In *Helianthus* the reaction is relatively sluggish and the contraction is not so great as in *Mimosa*. The difference between the two responsive reactions is one of degree and not of kind.

### 2. *Response to Stimulation of Adaxial and Abaxial Halves of the Organ.*

As stated before, the upper half of the pulvinus of *Mimosa* responds to application of light by local contraction; the leaf is thus erected and the movement towards light may be described as positive heliotropism. The leaflets attached to the sub-petioles are thus made to face the light. Under strong and long continued sunlight the excitation is transmitted across the pulvinus, and causes at first a neutralisation, and finally a reversed or

negative movement by the contraction of the more excitable lower half of the organ. This is the reason why the dia-heliotropic adjustment is less perfect under strong sunlight.

We obtain parallel reaction with *Helianthus*; here the petiole acts as an extended pulvinoid. Light applied from above causes an erectile movement; when applied below it causes a more energetic down movement. As the transverse conductivity of the petiole is feeble, the positive heliotropic response, induced by light acting from above, is rarely reversed into negative.

### 3. *The Mechanism of Heliotropic Curvature.*

A few words may now be said of the mechanics of curvature by which the stem of *Helianthus* bends towards light (fig. 1, *b*). All forms of stimuli, including that of light, induce a diminution of turgor and consequently contraction, and retardation of the rate of growth of the directly excited side. But this is not the only factor in bringing about the positive curvature. I have shown (4) that while the effect of direct stimulus at the proximal side of the stem induces diminution of turgor and contraction, its effect on the distal side, where it acts indirectly, is the very opposite, namely, an increase of turgor and expansion. The positive curvature is thus due to joint effects of direct and indirect stimulus at the two opposite sides. I have been able to demonstrate the induced increase of turgor at the distal side by experimenting with the stem of *Mimosa*. The stimulus of light is applied at a point directly opposite to the motile leaf, which by its movement indicates the change of turgor, the induced increase of turgor being indicated by an erection, and diminution of turgor by a fall of the leaf. Application of light at a point on one side of the stem was thus found to induce an increase of turgor at its diametrically opposite point.

Parallel experiments which I have recently carried out with *Helianthus* gave identical results. Arc light was continuously applied at a point opposite the indicating leaf; this induced an increase of turgor, as exhibited by a continuous erection of the leaf. We thus find that while direct stimulation induces a diminution of turgor at the proximal side, indirect stimulation causes an increase of turgor at the distal side. The positive heliotropic curvature is thus due to the joint effects of contraction of the proximal and expansion of the distal side.

### 4. *The Diurnal Movement.*

The daily periodic movements of the leaf *Mimosa* and of *Helianthus* exhibit a further similarity which is remarkable. I have shown elsewhere (5)

that in plants sensitive to light the operative factors in the diurnal movement are :—

*a.* The variation of geotropic action with changing temperature. A rise of temperature is found to inhibit the geotropic action ; a fall of temperature accentuates it. In consequence of this the leaf, subject to geotropic action, undergoes a periodic up-and-down movement ; the maximum fall of the leaf takes place at thermal noon, which is about 2 P.M., the maximum rise is at thermal dawn, about 6 A.M.

*b.* The action of light is, generally speaking, antagonistic to that of temperature. In the forenoon, rise of temperature causes a fall of the leaf, but continuous light acting from above tends to raise it. The rapid diminution of light towards evening acts virtually like a stimulus, causing an abrupt fall of the leaf.

The diurnal movements of *Mimosa* and *Helianthus* exhibit four phases which are very similar :—

(1) The leaf, owing to fall of temperature, erects itself from 2 to 5.30 P.M., or thereabouts.

(2) After 6 P.M. there is a rapid diminution of light, and the leaf undergoes a sudden fall, which continues till about 9 P.M.

(3) After 9 P.M. the leaf begins to erect itself with the fall of temperature, the maximum erection being attained at thermal dawn, which is at 6 A.M., approximately.

(4) In the forenoon the leaf is acted on by two antagonistic reactions, the effects of rising temperature and of increasing light, the effect of rise of temperature being predominant. The leaf thus continues to fall till thermal noon, which is about 2 P.M.

##### *5. Torsional Response to Lateral Stimulus.*

I shall now refer to a very important type of responsive movement induced by lateral stimulus. A stimulus is called lateral, when it acts either on the right or the left flank of a dorsiventral organ. I shall presently show that a dorsiventral organ responds to a lateral stimulus by torsion. That this effect is universal will be demonstrated by experiments on the “sensitive” *Mimosa*, and the “ordinary” plant *Helianthus*. In order to eliminate the effect of the weight of the leaf, and also for obtaining record of pure torsion, the petiole is enclosed in a hooked support of glass, with a smooth internal surface (fig. 2). Friction and the effect of weight are thus practically eliminated ; the circular support prevents any up or down movement, yet allows freedom for torsional response. I have recently

employed another device which is even more perfect. Instead of the tubular support, the petiole is slightly stretched in a horizontal direction by an attached thin elastic string of indiarubber tied to a rod. The up or down movement is thus prevented, whereas the string offers but feeble resistance to torsion. The torsion is magnified by an L-shaped piece of aluminium wire appropriately tied to the petiole, so that the long arm is at right angles to the petiole. The end of the arm is attached by a silk thread to the short arm of a recording lever, R; there is thus a compound

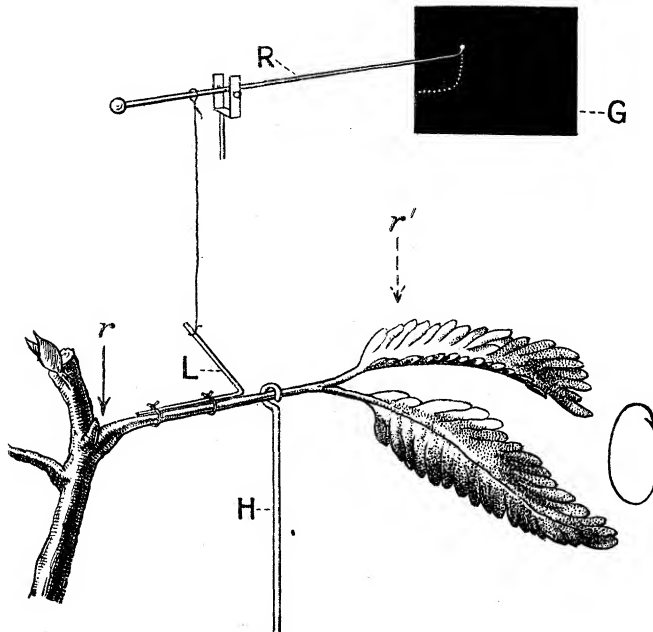


FIG. 2.—Diagrammatic representation for obtaining record of torsional response : H, hooked glass rod to secure pure torsional effect ; L, bent piece of metal for magnification of torsional movement ; R, recording lever ; G, oscillating smoked glass plate. Direct stimulation of the right flank,  $r$ , or indirect stimulation of the right sub-petiole,  $r'$ , induces right-handed torsion.

magnification of the torsional movement, a right-handed torsion producing an up-curve, and a left-handed torsion a down-curve. The oscillating recorder gives successive dots at definite intervals of time, which may be varied, according to requirements, from twenty to sixty seconds. Time relations of response may thus be obtained from the dotted record.

Fig. 2 gives a representation of the experimental method for studying the torsional response of various "sensitive" and ordinary leaves. Diverse stimuli are applied at one flank of the organ, which is the junction of the unequally excitable upper and lower halves of the pulvinus or petiole. We shall

presently find that the responsive reaction in all dorsiventral organs obeys a definite law in regard to the relation between the direction of incident stimulus and the resulting torsion. The torsion induced is either right-handed or left-handed, clockwise or anti-clockwise. In describing the direction of torsion, the position of the observer in regard to the plant must be definite; he should stand in front of the responding leaf and look at the central stem. When the right flank of the pulvinus or the petiole is struck by a horizontal beam of light  $r$ , coming from the right, the induced torsion is right-handed. Light acting on the left flank induces a torsion which is in the opposite or left-handed direction. On the cessation of stimulus the leaf recovers its normal position (fig. 3).

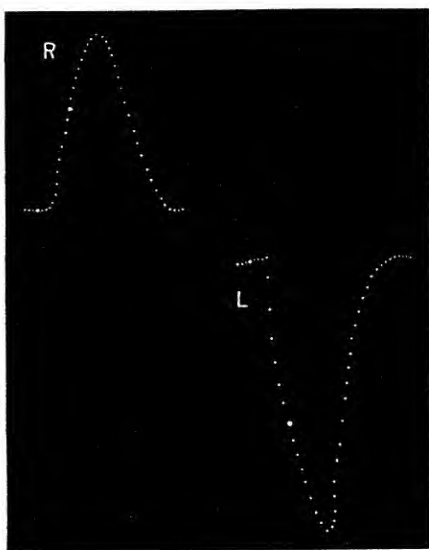


FIG. 3.—Record of torsional response of pulvinus of *Mimosa* by lateral light. Stimulation of the right flank induced right-handed torsion, R, represented by up-curve: stimulation of the left flank induced left-handed torsion, L. The two thick dots represent the duration of stimulus. Successive dots are at intervals of 20 seconds.

The response described above takes place when the pulvinus or the petiole is exposed to lateral light, the leaflets of the lamina being completely shielded from it. The differentially excitable organ thus undergoes a twist, in consequence of which the less excitable upper half of the pulvinus is made to face the stimulus. The leaflets or the lamina attached to the petiole are thus carried passively, like so many flags, to face the hypothetical source of light. It is obvious that the response is brought about by a definite physiological reaction and not for the utilitarian purpose of securing maximum illumination of the leaflets or the lamina. Teleo-

logical considerations, often adduced, offer no real explanation of the phenomena; such arguments are, moreover, highly misleading, for similar responsive torsion is induced, not merely by light, but by modes of stimulation so diverse as electrical, thermal, geotropic, and chemical.

Response of all anisotropic organs to lateral stimulus is included in the following generalisation:—

*An anisotropic organ, when laterally excited by any stimulus, undergoes torsion by which the less excitable side is made to face the stimulus.*

In a dorsiventral organ, it is the upper side which is, generally speaking, the less excitable. Hence the above generalisation may be expressed in the following simpler terms: Lateral stimulation of a dorsiventral organ induces a torsion which is right-handed, when the right flank is stimulated. Left-handed torsion is induced by the stimulation of the left flank.

*Torsional response of petiole of Helianthus.*—The above generalisation finds independent support from the response of the petiole of *Helianthus* to various stimuli applied laterally.

*Experiment 2.*—Two fine pins are thrust about 1 cm. apart on the right flank of the petiole of *Helianthus*, to serve as electrodes for application of induction shocks from a secondary coil; a similar pair of electrodes are attached to the left flank. On application of a feeble tetanising shock to the right flank, the petiole exhibited a right-handed torsion; stimulation of the left flank induced a left-handed torsion. Electric stimulation quickly stirs up the internal tissues, hence the latent period is short, and the responsive reaction is rapid (fig. 4, *a*). I next took a different specimen, and applied the stimulus of light to the right and the left flanks alternately. This gave rise to right- and left-handed torsions as under electric stimulus, the only difference being in the slower reaction and prolonged latent period (which was 15 minutes) (fig. 4, *b*). It must be remembered that in the case of light the excitation is gradually transmitted from the outer surface to the inner tissues. As regards the direct action of light, the results given above show that the responsive reactions of sensitive and ordinary plants are not different, but essentially similar. With reference to the heliotropic adjustment of leaves, we found that, when light strikes symmetrically in front, the leaf bends towards it. The growing stem itself is excitable, and its induced curvature is a contributory factor in placing the surface of the lamina at right angles to the light. Leaves struck laterally by light undergo torsion which is definite, being determined by the direction of the incident light. The torsion thus induced places the leaflets of the lamina at right angles to the light. These effects are produced, as stated before, when the

responding pulvinus or petiole are directly exposed to light, the leaflets and lamina being protected from it.

The heliotropic adjustment of leaves often takes place, as we have seen, when the motor organ is in the shade, or is artificially kept so. There must, therefore, be transmitted impulses by which the distant motor apparatus is so actuated that the leaflets or the lamina are placed at right angles to the light. The transmitted impulse, if single or diffuse, cannot evidently exert the necessary directive action. I shall presently show that the transmitted impulse is of a nervous character, that the impulses are more than one, and distinct from each other, and that they travel by different channels from the lamina which perceives light to the distant motor region where movement is effected in response to transmitted excitation.

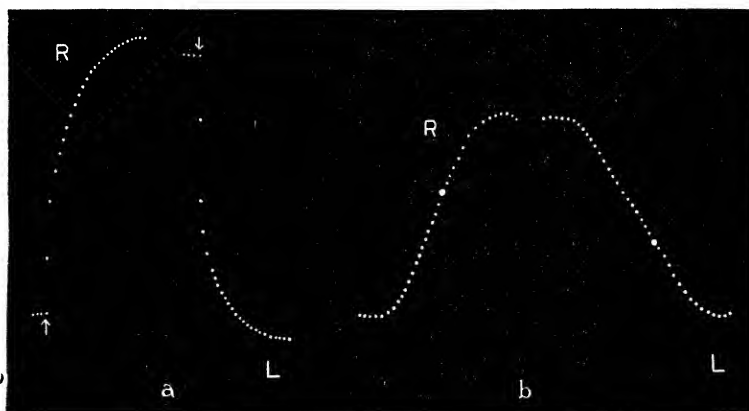


FIG. 4.—Torsional response of petiole of *Helianthus* in response to (a), electric stimulus, and (b), to stimulus of light. R and L are the opposite responses, due to stimulation of the right and left flanks. Successive dots are at intervals of 20 seconds. The prolonged latent period under light is not shown in the record. The portion of record exhibiting recovery is also omitted.

*The Complex Character of the Motor Organ.*—As regards the motor organ itself, I have stated that it is not simple but very complex. This will be understood from the following experiments on the pulvinus of *Mimosa*. Let us imagine the pulvinus to be diagonally divided into four quadrants. When the upper quadrant is subjected to light acting from above the responsive movement of the leaf is upwards; stimulation of the lower quadrant by light acting from below induces a down movement. The stimulation of the right quadrant (right flank) by a horizontal beam of light induces, as we have seen, a right-handed torsion; the left quadrant responds by a left-handed torsion. The four quadrants may, therefore, be regarded as four independent effectors,

the resulting movement being determined by their combined effects. We may distinguish these four effectors as the upper, the lower, the right and the left effectors. We shall presently find that these different effectors are set in action not merely by direct stimulation, but by the transmitted impulses from a distance, along definite conducting strands by which the different effectors are definitely innervated.

### III. THE NERVOUS MECHANISM IN PLANTS.

I shall now describe the "nervous" mechanism by which stimulus received at the receptive end gives rise to an excitatory impulse, which is conducted along certain definite channels. It is necessary here to justify the use of the terms nervous tissue and nervous impulse in regard to plants, since the idea has long been prevalent that there is nothing in plants which corresponds to the nervous impulse in animals. The transmitted effect of stimulus in *Mimosa* was thus regarded not as a propagated excitation but merely a hydro-dynamical disturbance. I have shown, however (7), that the transmitted impulse is of an excitatory character, that it may be blocked by various physiological blocks, and that, like the nervous impulse in animals, the velocity of transmission is enhanced with a rise, and depressed or even arrested by a fall of temperature.

#### 6. *Receptor, Conductor, and Effector.*

The nervous system of plants must be regarded as of a comparatively simple type. In speaking of the evolution of the nervous system, Parker points out that the contractile tissue or muscle appeared first as an independent effector, and that the nerve developed secondarily in conjunction with such muscles as a means of quickly setting them in action; that a receptor or sense organ alone would be of no service to an organism, neither would nerve or nerve centres alone; whereas a muscle cell or effector is of use if it can be stimulated directly (1).

In plants we find clear indications of these different stages. Thus in the leaf of *Erythrina indica*, and in the terminal leaflet of *Desmodium gyrans*, the pulvinus is the independent effector, the connecting nerve link being absent or functionally ineffective; heliotropic movement thus takes place when the pulvinus is directly stimulated, illumination of lamina having no effect. In *Mimosa* and in *Helianthus*, on the other hand, the intermediate nerve network has, as we shall find, become effective, the leaflets or the lamina serving as receptive organs. Haberlandt (9) has shown that in many cases the epidermal cells of leaves are of a lenticular shape, for increasing

the perception of light. He rightly observes that "in zoological nomenclature, organs concerned with the perception of external stimuli have always been known as sense organs, even among lower animals and in other cases in which it is doubtful if the organs in question are responsible for sensation in the psychological sense. It is, therefore, not only permissible, but necessary in the interest of consistency to apply the term sense organ to the analogous structure in plants."

With regard to nerve and nervous impulse, I quote the following from Bayliss (1), italicising the important passages:—

"We find the presence of nerve at a very early stage of evolution. . . . The effect of anything happening at one end of such a thread is conveyed with great rapidity to the other end of the nerve, wherever it may be. *Nerve fibres have no other function than that of carrying excitation.* When set into activity by some influence, the disturbances set up disappear spontaneously after a very short time if the stimulus ceases to act. . . . *It is usual to speak of a 'propagated disturbance' passing along the nerve, or sometimes a 'nervous impulse.'* The most sensitive apparatus has been able to detect with certainty one kind of change accompanying the passage of the propagated disturbance, namely, an electrical effect."

All the characteristics of nerve described above are also found in the conducting tissues of plants. As regards the velocity of transmission of impulse, it is not so high as in higher, but not so slow as in lower animals. Thus in the frog's nerve the velocity is about 32 metres per second; in *Eledone* it is, however, as low as 1 mm. per second. The velocity in *Mimosa* is about 30 mm. per second. Though the propagated disturbance causes no visible change, yet the nervous impulse in plant, as in animal, may be detected by definite electric change of galvanometric negativity; the disturbance set up disappears spontaneously on the cessation of stimulus. If the electric contact be made only at one point of the plant nerve, the other being at a distant indifferent region, the electric response is monophasic. But if the contacts are made at two points of the nerve, the proximal is the first to become galvanometrically negative; the propagated disturbance then reaches the distal point with concomitant negativity of that point. We thus obtain the characteristic diphasic response of the nerve (see below).

Since the nervous reactions in animals and plants are so essentially similar, delay in full recognition of this fact will undoubtedly retard the advance of science. I shall in the present paper demonstrate certain striking effects in plants, which at first sight would no doubt appear as very astonishing, but which in reality result from nervous reaction, usually regarded as the special characteristic of the animal. I shall be able to show that in the plant a

definite nervous link exists between the receptor and the effector, and that there is a well-developed system of innervation, by which the "attitude" of the plant-organ becomes adjusted to the incident stimulus.

#### *7. Localisation of Nervous Tissues in Plants.*

I have in my previous works shown that in *Mimosa* stimulus gives rise to an excitatory impulse, which is transmitted with a definite velocity, that this impulse has all the characteristics of the nervous impulse in animals. The most important problem in connection with this subject is the localisation of the conducting or nervous tissues. I succeeded in isolating a length of such a tissue in ferns and was able to obtain with it many results which are regarded as characteristic of nervous tissue in animals. In *Mimosa*, however, it is impossible to isolate the nervous tissues without injury, and I have for many years been confronted with the problem of localising *in situ* the particular tissue which serves as the conductor of excitation. I have recently been successful in my efforts, the method employed being that of the electric probe (6), by which I was able to localise the geotropic sense organ in plants.

Limitation of space enables me only to give the essential details of the method of localisation of nervous tissues and some typical results. A fuller account will be given in the forthcoming number of the 'Transactions' of my Institute.

The principle of the method will be understood if we take the somewhat analogous case of a cable along which electric messages are being transmitted. The conducting strand is here embedded in a non-conducting sheath. We can localise the embedded conductor and pick up the transmitted message by gradually thrusting in the electric probe, which is insulated except at the extreme tip. A galvanometer included in the circuit of the probe will begin to pick up messages that are being transmitted from the moment of contact of the tip of the probe with the conducting strand. The depth of insertion for contact can be read on a suitable scale and the position of the conductor may thus be determined.

We may similarly localise the exact position of the conducting nerve embedded in the petiole of *Mimosa* (fig. 5). Excitation of the sub-petiole will give rise to an excitatory impulse which travels in a centrifugal direction towards the stem. This excitatory impulse is of galvanometric negativity. The conducting nerve will be most intensely excited by the transmitted impulse, and the induced electrical change of this particular tissue will be maximum. Excitation will no doubt be irradiated to the adjoining tissue,

but this will undergo a rapid diminution in radial directions outwards. If the stimulus be moderate or feeble the irradiation will be slight.

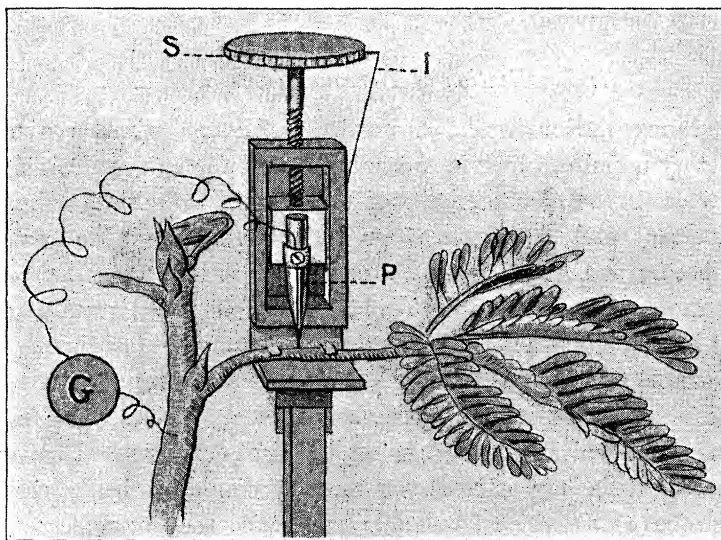


FIG. 5.—The Electric Probe for localisation of nervous tissue in plants. P, the probe in circuit with the galvanometer, G; S, the screw head, by the rotation of which the probe enters the petiole in successive steps; I, index by which the depth of intrusion may be determined.

The experimental procedure is as follows:—The probe is intruded perpendicularly along the diameter of the petiole. The intrusion of the probe is by steps, say of 0.05 or 0.1 mm. at a time. The slight wound produced by the insertion of the tip of the probe causes an excitation, which subsides completely in the course of about fifteen minutes. The sub-petioles are now stimulated by suitable stimuli, which may be chemical, thermal, mechanical or electric. The excitatory impulse is propagated preferentially along certain conducting channels in the petiole. The results to be described were obtained with all the different modes of stimulation. The electric mode of stimulation has the advantage that it can be maintained constant or varied in a graduated manner. Special precautions are taken that there should be no disturbance caused by leakage of the stimulating current; this is verified by the fact that reversal of primary current which actuates the secondary coil causes no change in the electric response; the excitatory electric change in different layers of tissue is, moreover, definitely related to the character of the tissue.

I shall anticipate results by describing the characteristic effects. The excitatory electric change detectable in different layers as the probe passes

from the epidermis to the central pith is found to rise suddenly to a maximum in the phloem portion of the fibro-vascular bundle; the xylem shows little or no transmitted excitation. Hence we arrive at the conclusion that it is the phloem which functions as the nerve of the plant. The characteristic electric maximum was not found in experiments where the probe missed the phloem; greater experience now enables me so to direct the passage of the probe as not to miss the nerve tract.

In the diagram of the transverse section of the petiole of *Mimosa* usually given in text-books there is in each bundle a single phloem strand outside the xylem. I was, therefore, considerably puzzled by the fact that in traversing the bundle I obtained two electric maxima, one before reaching the xylem, and the second after passing it. In order to determine the cause of this anomaly I made transverse sections of the petiole of *Mimosa*. Differential staining clearly brought out the fact that the phloem strand is not single but double, one above and the other below the xylem. The second electric maximum coincided with the inner phloem.

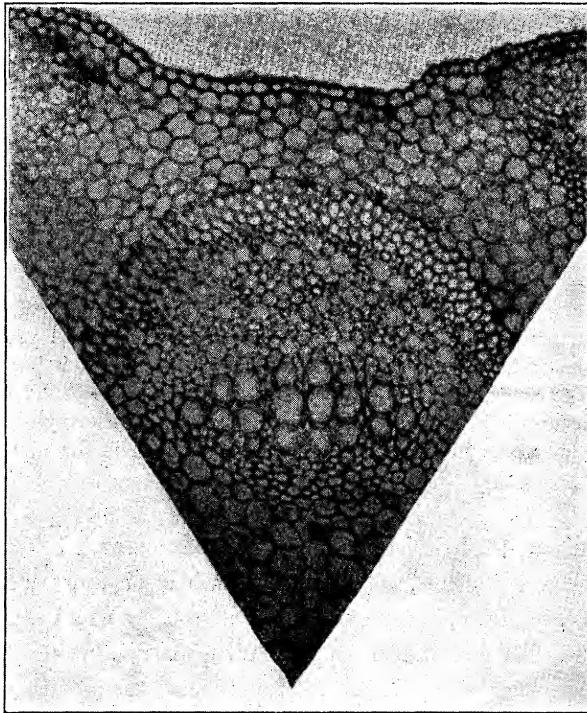


FIG. 6.—Micro-photograph showing a quadrant of the petiole and the fibro-vascular bundle. The tissues seen in the section are: the epidermis, the cortex, the bundle sheath, the first phloem, the xylem, the second phloem, and the central pith.

It may be stated here that in petioles provided with four sub-petioles there are four distinct bundles with four nerve trunks. But in specimens with two sub-petioles we only find two bundles, corresponding to the two sub-petioles. Two sub-petioles are found, generally speaking, in younger specimens. The micro-photograph (fig. 6) shows one of the bundles.

*Experiment 3.*—Electrical excitation in different layers: I shall now give detailed results of localisation of the conducting tissue. The probe enters the epidermis and is pushed in by steps of, say, 0.05 mm.; it passes in succession the cortex, C, the outer phloem, P, the xylem, X, the inner phloem, P', and the central pith, O. The thickness of the different layers is modified by age of the specimen. In the records given below (fig. 7) the electric response

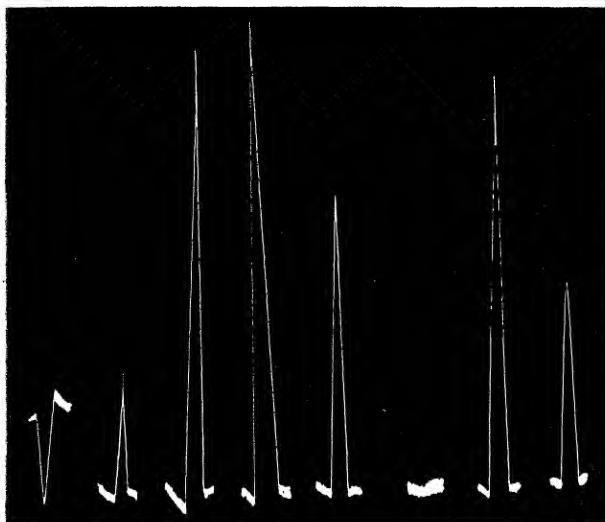


FIG. 7.—Galvanometric record of transmitted excitation in different layers of the petiole: the first is the positive response of the epidermis, the second is the feeble negative response of the cortex, the third, fourth, and the fifth are the enhanced responses in the first phloem, the sixth shows absence of excitation in the xylem, the seventh is the enhanced response in the second phloem, the eighth is the diminished response in the pith.

of the epidermis = +12 divisions of the galvanometer. I have shown elsewhere (8) that the epidermis, which protoplasmically is more or less dead, gives either a zero or a positive, in contradistinction to the normal negative response of living tissues. The probe at a depth of 0.1 mm. encountered the cortex and the response there was -17 divisions. The phloem extended through 0.15 mm., the average depth being 0.2 mm. The response in this region underwent a sudden enhancement, as seen in the three responses -61, -65 and -40 divisions. The xylem which was at a depth of 0.3 mm. showed no response,

proving that it was a non-conductor; when the probe reached a depth of 0.35 mm. it encountered the second phloem, where the response underwent a second enhancement of  $-56$  divisions. The probe reached the border of the pith at a depth of 0.4 mm. and the response underwent a diminution to  $-26$  divisions. In cases where the incident stimulus on the sub-petiole is feeble the irradiation effects are greatly diminished; the excitatory transmission is then found only in the phloem. I give below a summary of results obtained with ten different specimens:—

Table I.—Showing Intensity of Transmitted Excitation in Different Layers in Ten Different Specimens.

Different layers.	Transmitted excitation.										
	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	Mean.
Epidermis...	+1	0	0	0	0	0	0	+4	0	0	+0.5
Cortex .....	-2	-3	-50	0	0	0	0	0	0	0	-5.5
Phloem .....	-30	-30	-100	-30	-36	-44	-33	-18	-20	-24	-36.5
Xylem .....	-8	-9	0	0	0	-10	0	-4	-8	-8	-4.7
Phloem .....	-30	-30	-84	-10	-36	-20	-12	-18	-20	-16	-26.8
Pith .....	0	-6	-29	0	0	-7	0	0	0	0	-4.2

It will be seen that in all cases the phloem is invariably found to be the best channel for conduction of excitation. The following curve (fig. 8),

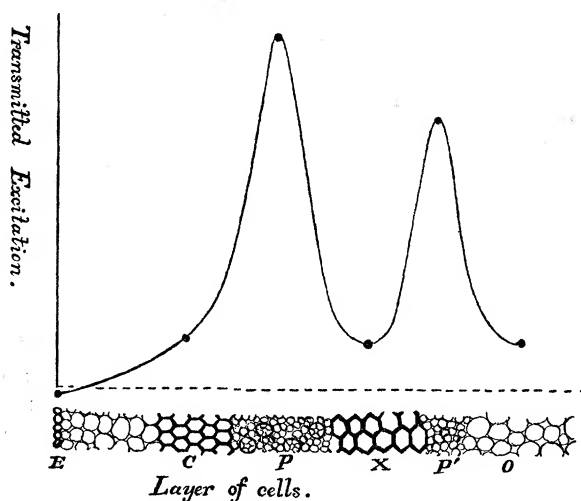


FIG. 8.—Curve showing the different intensities of transmitted excitation in different layers: E, epidermis; C, cortex; P, first phloem; X, xylem; P', second phloem; O, pith.

plotted from the mean values given in Table I, illustrates this in a striking manner.

#### IV. THE TRANSMITTED NERVOUS IMPULSE.

In certain experiments with petioles having four bundles, I allowed the probe to pass vertically through the petiole when it encountered the upper and lower bundles. I thus obtained maximum transmitted excitations in the phloems of the upper fibro-vascular bundle, and a similar maximum in the phloems of the lower bundle, the intervening layers of tissue being practically non-conducting. From this it follows that excitatory impulse is propagated along definite channels through the length of the petiole.

##### 8. *Definite Innervation.*

We shall now follow the nervous strand from the perceptive lamina to the motor organ. In *Mimosa*, the leaflets attached to the sub-petioles form the perceptive area for light. The excitation is conducted along the phloem strand of the sub-petiole, and thence through the connected phloem in the petiole. In leaves with four sub-petioles there are, as stated before, four main bundles which reach the motile organ, the pulvinus. There the fibro-vascular bundles apparently fuse, but very fine section of the pulvinus shows lines of separation. In any case, I shall be able to show that nervous strands are physiologically distinct. These terminate in the four effectors, of which two are lateral, the right and the left effectors; the other two are upper and lower effectors. In younger specimens of *Mimosa* there are two sub-petioles instead of four, and the two nerve strands are continued to the right and left flanks of the pulvinus, the particular innervation being to the right and left effectors respectively. In *Helianthus*, the right and left nerve pass along the right and left flank of the petiole, which, as we have seen, serves as an extended motor organ. The following results will show that these strands function as distinct nerves:—

*Experiment 4.*—One electrode was pricked in so as to make contact with the phloem of the right bundle embedded in the petiole; the second contact was made with a distant indifferent point. Electric stimulation of the right vein of the lamina of *Helianthus* gave rise to electric response of galvanometric negativity, the response being mono-phasic. Application of thermal and chemical stimulus produced similar results (fig. 9).

*Experiment 5.*—The second electrode was in this case thrust into the nerve of the plant about 1 cm. behind the first electrode. The response is

now diphasic, since excitation reached the two points in succession (fig. 9). Discontinuity of the nerve stops the transmitted impulse, as will be seen below.

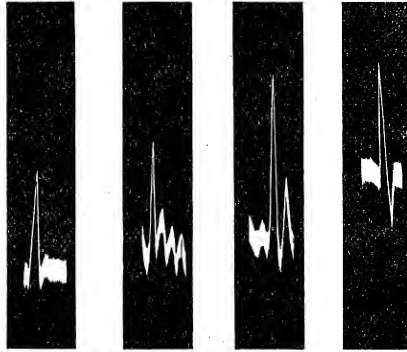


Fig. 9.—Galvanometric record of transmitted excitation in the nerve of *Helianthus*. The first is in response to electric stimulus, the second and the third to thermal and chemical stimulus. Note in these multiple responses due to strong stimulation. The fourth exhibits diphasic response (see text).

#### 9. *The Directive Action of Propagated Impulse in Heliotropic Leaf-adjustment.*

In *Mimosa* and in *Helianthus* I have traced the nervous channels from the receptor to the effector, and showed how the nervous impulse is propagated along definite channels. The most difficult problem that confronts us now is to explain the responsive movement and torsion of the motor organ, by which the expanded leaf surface faces the light. I shall now describe the motor reaction when different parts of the leaf surface are locally stimulated, not only by light, but by diverse modes of stimulation.

##### (a) *Mimosa pudica.*

*Experiment 6.*—For this experiment I first took specimens of *Mimosa* leaf having two sub-petioles. The right sub-petiole was stimulated by feeble tetanising electric shock. The response was by right-handed torsion. The latent period was 2 seconds, and the torsional movement continued for 20 seconds, even on cessation of the stimulus, after which there was a slow recovery, not shown in the record (fig. 10, *a*). The propagated impulse has thus followed its definite path, and reached the right flank of the pulvinus or the right-effector. We saw that the characteristic response of this particular effector is by a right-handed torsion. Thus the same response takes place, whether the effector is directly stimulated or by transmitted excitation. This finds strongest confirmation from the following experiment, where the responsive movement is made to undergo reversal.

*Experiment 7.*—The left sub-petiole was now stimulated by feeble tetanising shock, as in the last experiment. The response was now by a left-handed torsion (fig. 10, *a*); the nervous impulse now reached the left flank of the pulvinus, or the left-effector, the characteristic response of which is by a left-handed torsion. The leaf may thus be twisted to the right or to the left by alternate stimulation of the two sub-petioles. A feeble tetanising shock should be used for these experiments, since a strong excitation becomes diffused as it reaches the fibro-vascular ring in the pulvinus, and the predominant excitation of the entire lower half would then mask the characteristic effects of the right or the left effectors. As

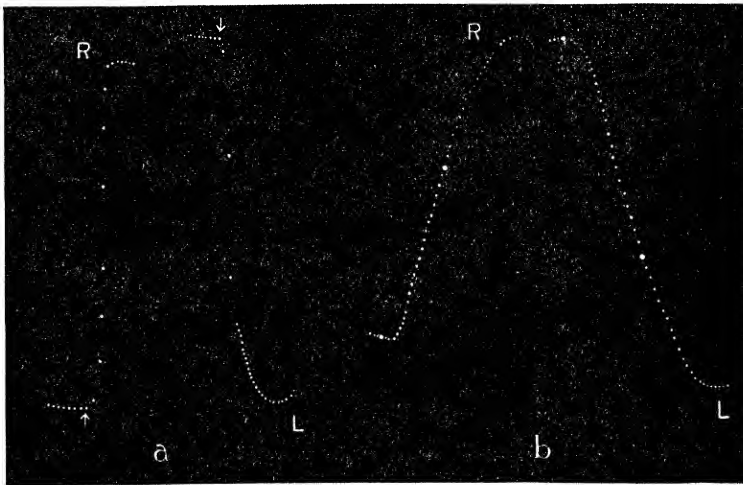


FIG. 10.—Responsive torsion by transmitted excitation in *Mimosa* under (*a*), electric stimulus; (*b*), under stimulus of light. Note right-handed and left-handed torsions by stimulation of the right and left sub-petioles. Successive dots in (*a*) are at intervals of 2 seconds, and in (*b*) 20 seconds. Note the quick reaction under electric, and slower reaction under photic stimulation.

regards leaves with four sub-petioles, we shall presently find that they transmit definite impulses to the four quadrants of the pulvinus, to the right and to the left, to the upper and the lower effectors, thus giving rise to definite reflexes.

*Experiment 8.*—Stimulus of Light.—I next tried the action of stimulus of light on the leaflets of the right sub-petiole; here also the transmitted excitation induced a right-handed torsion. The latent period was, for reasons explained before, longer than in the case of electric stimulation. It should be remembered that the light was applied vertically, and the responsive torsion was such that the amount of light absorbed by the

leaflets became reduced by the torsion. Hence it is obvious that it is not the advantage of the plant, but the inevitable physiological reaction, that determines the movement. Stimulation of the leaflets of the left sub-petiole induced a left-handed torsion. When the leaflets of both the sub-petioles were illuminated by vertical light, the two resulting torsions balanced each other. While in this state of dynamic balance, if the intensity of light on one of the sides, say the left, be diminished by interposition of a piece of

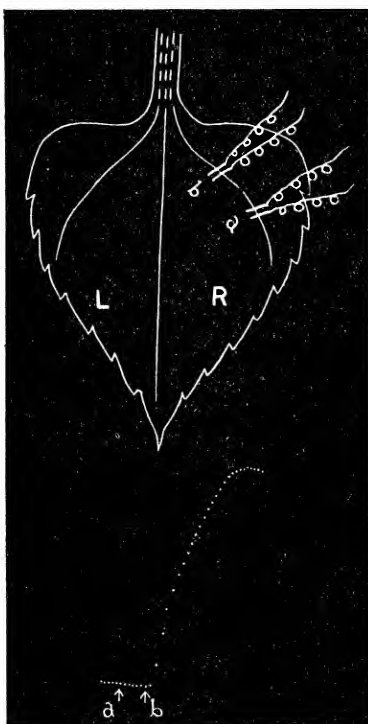


FIG. 11.—The upper figure is a diagram of stimulation of nerve-endings of *Helianthus*. The record below shows that stimulation beyond the cut gives (*a*), no response ; while stimulation at *b*, induces right-handed torsion.

paper, the balance is at once upset, and we find a right-handed torsion. It is thus seen that equilibrium is only possible when the entire leaf-surface (consisting of the two rows of the leaflets) is equally illuminated ; and that would be the case when the surface is perpendicular to the incident light. The dia-heliotropic attitudes of leaves is thus brought about by distinct nervous impulses, initiated at the perceptive region actuating the different effectors.

In the case of leaves with four sub-petioles, illumination of the extreme

right induces, as already stated, a right-handed torsion; that of the second sub-petiole from the right brings about a movement of erection; the stimulation of the third causes a down movement, while that of the extreme left causes a left-handed torsion. The leaf is thus adjusted in space by co-ordinated action of four distinct reflexes.

(b) *Helianthus annuus*.

Results in every way similar are obtained with leaf of *Helianthus*. Here we can distinguish three main veins or nerves, which collect excitation from different regions of the lamina.

*Experiment 9*.—I first tried electric stimulation. The insertions of the electrodes were made in the manner shown in the diagram (fig. 11).

*Experiment 10*.—Effect of Discontinuity.—A cut is made between *a* and *b*, thus interrupting the continuity of the nerve. Electric stimulation at *a* induced no responsive movement; stimulation at *b* induced, however, the normal response by right-handed torsion (lower record fig. 11).

*Experiment 11*.—Alternate Electric Stimulation.—The right and left nerve endings in the lamina were stimulated alternately. This gave rise to right-handed and left-handed torsions respectively. In fig. 12, *a*, is given the record of right-handed torsion.

The following experiments will show that photic stimulus induces a reaction which is similar to that of electric stimulus:—

*Experiment 12*.—Stimulus of Light.—Sunlight was thrown first on the right half and then on the left half of the lamina. The transmitted excitations induced corresponding torsional responses (fig. 12, *b*). A balance was produced when the two halves of the lamina were simultaneously exposed to equal illumination. Here also, as in *Mimosa*, the heliotropic adjustment is brought about by balanced reactions of the different effectors.

The movement of a dia-heliotropic lamina has been figuratively compared with the movement of the human eye by which it points itself to a luminous object. It is strange that there is more truth in this comparison than was suspected. In describing the rolling of the eyeball Bayliss says (1): "When there are two sets of muscles acting on a movable organ, such as the eye or a part of a limb, in such a way that they antagonise one another, it is clear that for effective performance of a particular reflex movement, any contraction of the muscles opposing this movement must be inhibited. Further, the inhibition of one group must proceed *pari passu* with the excitation of the other group to ensure a well-controlled and steady motion."

Now, in the torsional adjustment of the leaf due to unequal stimulation of the two receptors—the right and left halves of the lamina—let us take the

extreme case where one half, say the right, is alone stimulated, either by light or by electric shock. The two effectors for torsional movement, the right and the left, are the responding tissues in the right and left flanks of the petiole. These are actuated by the nervous impulses transmitted along the two conducting strands. When the right half of the lamina is stimulated the transmission of excitation along the conducting strand on the right is detected (Experiment 5) by an electric change of galvanometric negativity, and the corresponding mechanical response of the right effector is, as shown before, by a right-handed torsion. We may next inquire the nature of the transmitted impulse along the left flank of the petiole concomitant with the

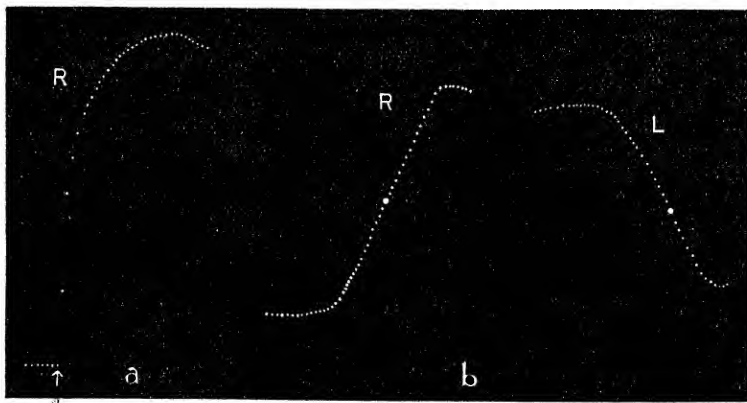


FIG. 12.—Torsional response due to transmitted excitation in *Helianthus*: (a), right-handed torsion due to electric stimulation of the nerve-ending in the right half of the lamina; (b), right-handed and left-handed torsions due to transmitted excitations caused by alternate illumination of the right and left half of the lamina. Light was stopped after the thick dot.

excitation of the right half of the lamina. It is obvious that a similar excitatory impulse on the left flank (the electric indication of which is galvanometric negativity) would oppose and thus neutralise the particular directive movement. Hence for ensuring a steady directive motion, in response to stimulation of the right half of the lamina, all excitatory impulse to the left flank of the petiole should be inhibited. Further, the directive movement induced by the stimulation of the right half of the lamina would be actively helped if the motor reaction of the left flank of the petiole be of an opposite character to that in the right flank. We found that the right-handed torsion is induced by a differential contraction of the right flank and for concordant effect the reaction of the left flank should be opposite, *i.e.*, a differential expansion. The nervous impulse which actuates the right

effector when the right half of the lamina is alone stimulated, is indicated by galvanometric negativity; for concordant movement under the above condition, the impulse which actuates the left effector should be of opposite sign, *i.e.*, of galvanometric positivity.

I carried out two sets of experiments on the above lines with an identical leaf of *Helianthus*. First, I carried out the usual experiment of the electric detection of transmitted excitatory impulse. In this, one of the contacts was made with the right nerve in the petiole, the second being with a distant indifferent point. The nerve endings on the right half of the lamina were electrically stimulated and the transmitted impulse along the nerve gave the usual excitatory reaction of galvanometric negativity. A second pair of contacts were made for detection of transmitted impulse in the nerve of the left flank of the petiole. Stimulation of the nerve termination of the right half of the lamina gave in the left nerve a reaction of galvanometric positivity. In practice stimulus was always applied to the right half of the lamina, and galvanometric connections were made alternately with the right and left nerve. The results were always the same and showed that excitation of a nerve gave rise to an opposite reaction in the contiguous nerve. There is no doubt that these two nervous impulses of opposite signs reaching the antagonistic tissues of the two flanks of the motor organ must be of importance in the co-ordination of the resulting movements.

#### *General Summary.*

In certain leaves the heliotropic adjustment is brought about by transmission of nervous impulse to the motor organ. A continuity is shown to exist in the response of "sensitive" and ordinary plants. *Mimosa pudica* is taken as a type of the former, and *Helianthus annuus* of the latter. Mechanical response is brought about in both by the differential excitability of the upper and lower halves of the motile organ. The lower half in both is the more excitable. Local stimulation of the abaxial half of the organ induces an erectile movement, that of adaxial half a more rapid downward movement.

Heliotropic curvature of a stem is due to the joint effects of contractile reaction of the proximal and expansion of the distal side.

The daily periodic movements of the leaves of *Mimosa* and of *Helianthus* are essentially similar. The diurnal movement is brought about by the variation of the geotropic action with changing temperature, and by the varying intensity of light. The leaves erect themselves during the fall of temperature from thermal noon at 2 P.M. to about 5.30 P.M. Owing to the rapid diminution of light in the evening the leaves undergo an abrupt fall

which continues till 9 P.M. After this the leaves erect themselves, till the maximum erection is attained at 6 A.M., which is the thermal dawn. The movement of the leaves is then reversed and there is a continuous fall till the thermal noon at 2 P.M.

A very important motile reaction in the adjustment of leaves is the torsional response to lateral stimulus. The following is the law which determines the directive movement: An anisotropic organ when laterally stimulated by any stimulus undergoes torsion by which the less excitable side is made to face the stimulus. In a dorsi-ventral organ the upper side is, generally speaking, the less excitable side, and the response of such an organ to lateral stimulus may be expressed in the following simple terms. Lateral stimulation of a dorsiventral organ induces a torsion which is right-handed, when the right flank is stimulated. Left-handed torsion is induced by the stimulation of the left flank.

The effects described above take place by direct stimulation of light. They also take place under transmitted excitation.

The motor organ may be regarded as consisting of four effectors; the response of the right effector is by a right-handed torsion, and of the left effector by a left-handed torsion. The upper and lower effectors respond by rectilinear up-and-down movements.

The nervous tissue in plants was localised by means of the Electric Probe which was made to pass by successive steps through the petiole. The maximum transmitted excitation was localised at the phloem portion of the fibro-vascular bundle. Hence the phloem functions as the nerve of the plant.

Excitation at the receptive region is propagated along a definite conducting channel, which is traced from the receptive area in the lamina to the corresponding effector in the motor region.

In a petiole of *Mimosa*, provided with two sub-petioles carrying rows of leaflets, stimulation of the right row of leaflets by light gives rise to an excitatory impulse which reaches the right effector and induces a right-handed torsion. Stimulation of the left row of leaflets induces the opposite, or left-handed torsion. When both the sub-petioles are illuminated equilibrium is only possible when the entire leaf surface (consisting of the two rows of leaflets) is perpendicular to the incident light. The dia-heliotropic attitude of leaves is thus brought about by distinct nervous impulses initiated at the perceptive region actuating the different effectors.

In *Mimosa* with four sub-petioles, illumination of the second sub-petiole induces an up-movement; that of the third sub-petiole a down-movement. The leaf is thus adjusted in space by the co-ordinated action of four reflexes.

Results similar to the above were also obtained with *Helianthus*.

For the movement of the eye the contraction of the muscle opposing the movement has to be inhibited. In the torsional movement of the leaf it is found that the stimulation of one nerve causes in a contiguous nerve an opposite reaction. The nervous impulses of opposite signs reaching different flanks of the motile organ is thus of importance in the co-ordination of the resulting movement.

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*The Ultra-Violet Absorption Spectra and the Optical Rotation of the Proteins of Blood Sera.*

By S. JUDD LEWIS, D.Sc. (Tübingen), B.Sc. (London), F.I.C.

(Communicated by Prof. J. N. Collie, F.R.S. Received April 29, 1921.)

The earlier part of this investigation was described in a paper entitled "The Ultra-Violet Absorption Spectra of Blood Sera," communicated by Sir William Ramsay, K.C.B., to the Royal Society in 1916 and published in the 'Proceedings' (series B, Vol. 89, pp. 327 to 335).

At the close of the paper, attention was directed to the inadequacy of the sector spectrophotometers then available, and reference was made to one of new design then under construction. In the meantime, a full description of this instrument has been published in a paper entitled "A New Sector Spectrophotometer" by the present writer, in the 'Transactions of the Chemical Society' (1919, vol. 115, pp. 312 to 319), together with figure and diagrams. With this instrument completely satisfactory results have been obtained, and with it most of the work now to be described has been done.

The earlier work had reference to serum as a whole; and as foreshadowed



FIG. 1.—Dia-heliotropic adjustment of leaves : (a), in *Mimosa* ; (b), in *Helianthus annuus* ; and (c), in a different species of *Helianthus*. (From photographs.)

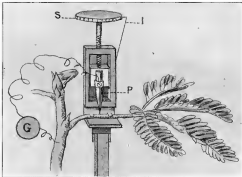


FIG. 5.—The Electric Probe for localisation of nervous tissue in plants. *P*, the probe in circuit with the galvanometer, *G*; *S*, the screw head, by the rotation of which the probe enters the petiole in successive steps; *I*, index by which the depth of intrusion may be determined.

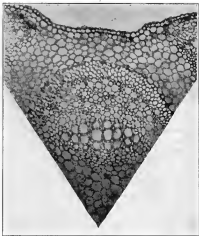


FIG. 6.—Micro-photograph showing a quadrant of the petiole and the fibre-vascular bundle. The tissues seen in the section are: the epidermis, the cortex, the bundle sheath, the first phloem, the xylem, the second phloem, and the central pith.